DENTITIONAL DIVERSITY IN *RHACODACTYLUS* (REPTILIA: GEKKONIDAE)

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The teeth of gekkonid lizards have long (and erroneously) been considered to be simple, homodont, isodont and conical. Although some previously held beliefs about gecko dentition are largely true, the immense variability expressed among the approximately 900 species precludes the applicability of most generalities. A particularly wide range of tooth types is seen in the carphodactyline gecko genus *Rhacodactylus* (including those Australian forms previously assigned to the genus *Pseudothecadactylus*).

Rhacodactylus auriculatus is characterised by huge caniniform teeth that are few in number and widely-spaced. There is a steady increase with body size in the number of tooth loci in juveniles of this species (after the loss of the egg teeth). The pointed uni- or bicuspid teeth in this taxon are only slightly recurved and are constricted at the crown base. In *R. leachianus* and *R. trachyrhynchus* the teeth are decidedly recurved and present a long, blade-like occlusal surface. The teeth of other members of the genus are smaller and much more numerous (up to 180+ marginal tooth loci). Teeth in these forms may be uni- or bicuspid and typically have short crowns, either conical or with moderately pronounced occlusal ridges.

Dental anatomy in *Rhacodactylus* appears largely unrelated to phylogeny. Rather, the teeth correspond to dietary preferences. Many tooth designs are capable of processing insect prey but the caniniform teeth of *R. auriculatus* and the recurved teeth of some of its congeners seem to be specialisations for feeding on vertebrates and other soft-bodied prey. Dietary data, though fragmentary, supports this interpretation. ☐ *Gekkonidae, Rhacodactylus, dentition, diet, phylogeny, functional morphology.*

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The teeth of gekkonid lizards have been characterised as small, numerous, pleurodont, homodont, and pointed (Kluge, 1967). This generalisation has, however, not withstood the input of new data gained through more detailed analyses of dental morphology. Variation in tooth structure among the approximately 900 species of geckos is marked and has most recently been evaluated by Sumida and Murphy (1987) who identified several morphologies, including both bicuspid and quadricuspid tooth crowns.

Among the generalisations about gekkonid dentition that do hold true are that the teeth are pleurodont and, relative to most lizards, very numerous (see Edmund, 1969; Vorobyeva and Chugunova, 1986 for representative tooth counts for selected lizard groups). One species of gekkonine gecko, *Uroplatus fimbriatus*, may have more marginal teeth than any other living amniote (Bauer and Russell, 1989). Tooth number in geckos increases with age and the concomitant increase in the length of the germinal tooth bed or dental lamina (Kluge, 1962; Edmund, 1969). Like most lizards with determinate growth, adult tooth number in geckos stabilises around a particular species mode (Owen, 1866) although variance may be quite high.

All geckos bear teeth only on the maxillae, premaxillae and dentaries (Sumida and Murphy, 1987). Tooth size generally increases from posterior to anterior within a tooth-bearing element, but in at least one species, *Teratoscincus scincus*, the largest teeth are in the middle of the tooth rows (Edmund, 1969). Tooth replacement and addition of new loci is believed to proceed from back to front in waves affecting alternating positions in accordance with Edmund's Zahnreihen theory (Edmund 1960, 1969; Osborn, 1973, 1975; Kline 1983; Kline and Cullum, 1984, 1985), although most evidence for this pattern comes from other lizard groups. In addition to the typical adult dentition, all oviparous geckos also exhibit embryonic egg teeth (Kluge, 1967) which drop out shortly after hatching (Ananjeva and Orlov, 1986). The paired condition of gekkonid (including pygopodid) egg teeth appears to be a uniquely derived condition for the group (Kluge, 1967, 1987; Ananjeva and Orlov, 1986).

During the course of revision of the carphodactyline geckos of the Southwest Pacific (Bauer, 1986) we noted a unique dental morphology characterising the New Caledonian forest gecko, *Rhacodactylus auriculatus* - the possession of enlarged, pointed caniniform 'fangs'. This taxon is one of 44 in the tribe Carphodactylini, a monophyletic group of poorly known geckos endemic to Australia, New Zealand and New Caledonia. *Rhacodactylus* is of particular interest because the genus consists of moderately to very large species that are capable of taking prey types outside of the range normally available to other geckos. Further, *Rhacodactylus* (including the Australian geckos previously assigned to the genus *Pseudothecadactylus*) occupies a fairly wide range of habitat types, from the Arnhem Land escarpment to the rainforests of eastern New Caledonia. In New Caledonia, in particular, members of the genus have few competitors and may be considered the primary non-volant predators. In light of the implications of *Rhacodactylus* biology for dental form and a renewed interest in gekkonoid tooth form and function in general (e.g. Patchell and Shine 1986a,b; Sumida and Murphy, 1987) we take this opportunity to present an analysis of the descriptive and functional anatomy of the teeth in the genus *Rhacodactylus*.

MATERIALS AND METHODS

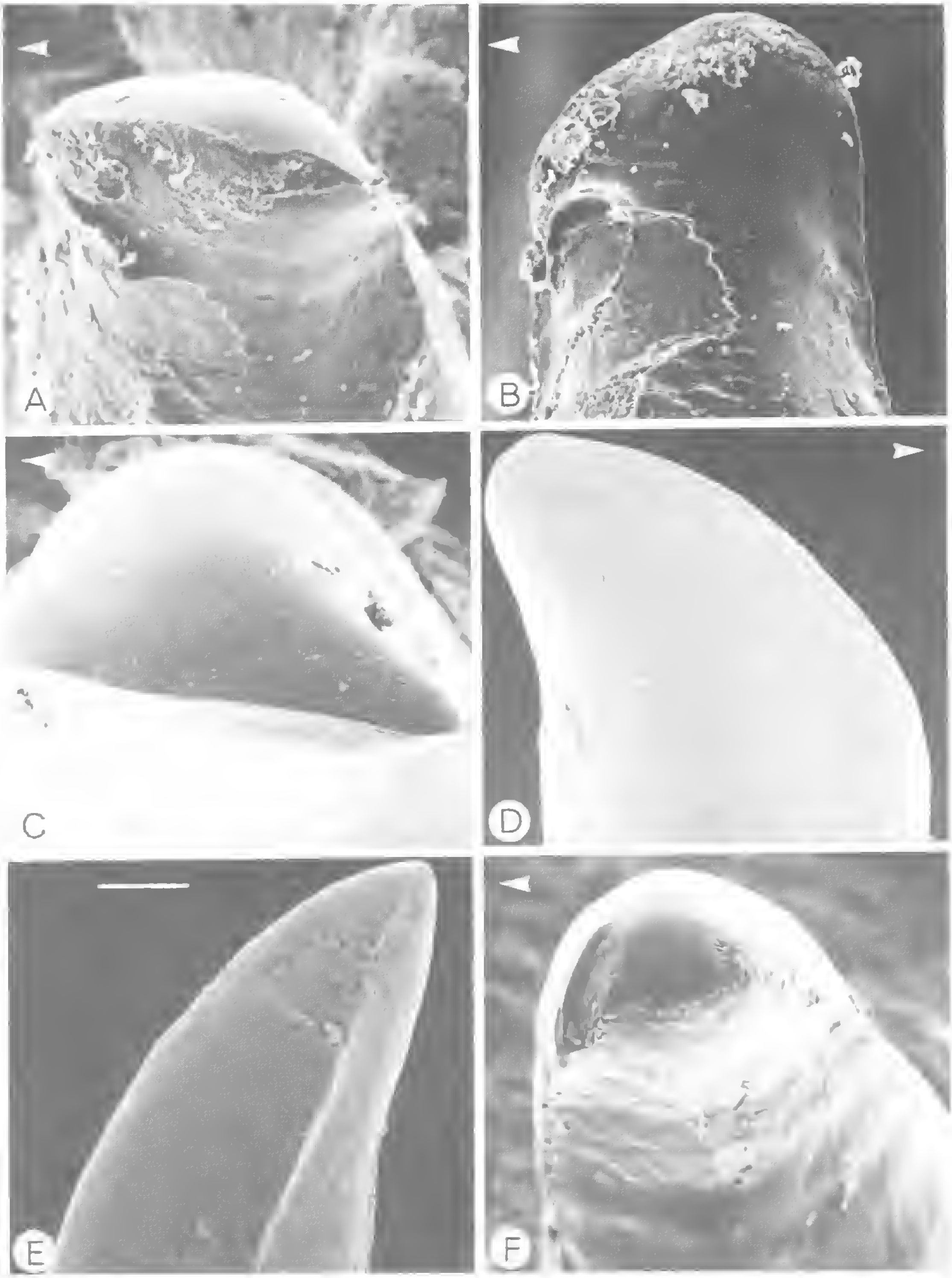
Dentition was examined in adult skeletal and cleared-and-stained specimens of five of the six recognised species of New Caledonian *Rhacodactylus* as follows: *R. auriculatus* (10 specimens), *R. chahoua* (1 specimen), *R. ciliatus* (1 specimen), *R. leachianus* (1 specimen), *R. trachyrhynchus* (1 specimen). In addition, one cleared and stained pre-hatchling of *R. auriculatus* was also examined. Vascularization of the dental lamina was also observed in a number of cleared and stained adult *R. auriculatus* which had been injected with Microfil^{TM} medium (see Russell et al., 1987, 1988). Radiographs of all of the above-mentioned taxa, as well as *R. sarasinorum* and the Australian members of the genus, *Rhacodactylus* (*Pseudothecadactylus*) *australis* and *R.* (*P.*) *lindneri*, were examined and spirit-preserved specimens of most taxa were also consulted. Specimens were borrowed from the collections of the California Academy of Sciences (CAS), the British Museum (Natural History) (BM(NH)), the Australian Museum (AMS) and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Tooth counts for these taxa are expressed in terms of tooth loci, since teeth themselves may be lost or damaged post mortem. For comparative purposes reference was made to dry skeletal, cleared-and-stained and radiographic material representing all gekkonid genera except *Microscalabotes* and *Paragehyra*. Skeletal material was examined under a binocular microscope and individual teeth were removed, sputter- coated with gold-palladium alloy and examined with an Hitachi S–450 scanning electron microscope. Photomicrographs were taken on a Wild stereo dissecting microscope with camera mount or with a 35mm camera with macro lens.

RESULTS

TOOTH MORPHOLOGY

In *Rhacodactylus chahoua*, *R. ciliatus*, *R. sarasinorum* and the Australian species *R.* (*Pseudothecadactylus*) *australis* and *R.* (*P.*) *lindneri*, the tooth crowns are short, relatively blunt, and generally peg-like. All teeth are somewhat labio- lingually compressed, with the labial face of each tooth exhibiting a marked convex bowing. The lingual surface is somewhat more perpendicular with respect to the tooth-bearing bone. In *R. ciliatus* the crown is distinctly

FIG. 1.A. Maxillary tooth of *Rhacodactylus chahoua* (CAS 167764), occlusal view. Arrow in this and subsequent figures represents anterior direction. B. Same specimen as A, labial view showing asymmetrical crown height. C. Maxillary tooth of *Rhacodactylus leachianus* (CAS 167890), occlusal view showing elongate narrow cutting ridge. D. Same specimen, labial view showing pronounced recurvature of the tooth crown. E. Oblique view of maxillary tooth of *Rhacodactylus auriculatus* (CAS 165891) illustrating pointed tooth crown and lateral extension of single cusp. F. Same specimen as E, occlusal view showing the dorsally directed single cusp and general smoothness of the tooth. Scale bars for all figures = 100μm.


A
B
C
D
E
F

bicuspid, with a shallow trough separating the higher and more pronounced labial cusp from its lingual counterpart. In *R. chahoua* the tooth crown is basically unicuspid (Fig. 1A), although older, more worn teeth may exhibit a weakly demarcated lingual 'shoulder'. In the remaining taxa the teeth have weakly developed cusps or are conical with a rather blunt point. The latter condition is especially true of younger teeth at the posteriormost loci. In all taxa, but most notably in *Rhacodactylus chahoua*, the tooth crowns are directed somewhat posteriorly (Fig. 1B) and the posterior portion of the cusp(s) rise(s) slightly higher above the gum line. In *R. chahoua* the largest teeth are at the level of the posterior border of the nostril, in the anterior portion of the maxillae. The premaxillary teeth are uniformly small, but similar in morphology to those of the maxillae and dentaries. *Rhacodactylus sarasinorum*, *R. ciliatus* and the *Pseudothecadactylus* species are characterised by isodonty.

In the largest species of *Rhacodactylus*, *R. leachianus* and *R. trachyrhynchus*, teeth at the posterior (younger) loci are generally similar in appearance to those of *R. chahoua*. Anteriorly, however, the teeth are elongate and their crowns are decidedly angled. In *R. leachianus* the crown presents a very long and narrow occlusal blade (Fig. 1C). The highest (posteriormost) point of the crown projects backwards beyond the plane of the crown base as a rounded hook (Fig. 1D). There are no multicuspid teeth in this taxon. In *R. trachyrhynchus* the anterior teeth are only slightly curved and do exhibit a lingual 'shoulder' or weak cusp. As in *R. chahoua* the largest teeth in both *R. trachyrhynchus* and *R. leachianus* are in the anterior part of the maxillae but in the former species, the premaxillary teeth are also quite large.

A third type of morphology is exhibited by *Rhacodactylus auriculatus*. In this taxon all of the teeth are elongate and sharply pointed (Fig. 1E). The crown is only slightly inflected. Although most teeth appear to be unicuspid (Fig. 1F), a faint lingual cusp characterises some of the teeth in anterior loci of all tooth-bearing bones. Unlike other *Rhacodactylus* species, some of the teeth of *R. auriculatus* are constricted at the junction of root and crown (Fig. 2). This condition does not occur in the premaxillary teeth and is most evident in the teeth occupying older, anterior maxillary and dentary loci.

No surface microstructures, such as grooves or serrations, were located on the teeth of any species *Rhacodactylus*. Likewise, the teeth of upper and lower jaws do not normally contact one another in occlusion.

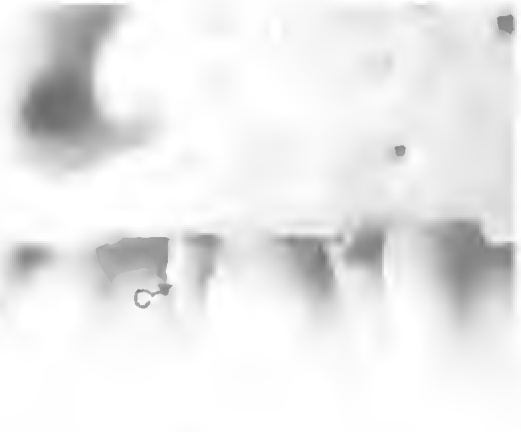


FIG. 2. Anterior portion of left maxilla of *Rhacodactylus auriculatus* (CAS 165891) showing the constriction (c) of the teeth at the junction of crown and root.

TOOTH SIZE, NUMBER AND REPLACEMENT

There is a two-fold difference in marginal tooth locus number in mature individuals of *Rhacodactylus* spp. Total locus number ranges from a mean of 105.5 in *R. auriculatus* to over 180 in *R. sarasinorum*. Figure 3 shows the distribution of marginal tooth loci versus skull length for mature specimens for which total counts could be made umambiguously. Although sample sizes for all taxa except *R. auriculatus* are very small, qualitative differences among species are evident. (Unfortunately the two specimens of *R. trachyrhynchus* examined were sub-adults and thus the data for this taxon are not strictly comparable to those derived from other specimens.) *Rhacodactylus sarasinorum*, *R. ciliatus* (Fig. 4A) and the two *Pseudothecadactylus* have the smallest skull (and body) size, yet they exhibit the greatest tooth number. The remaining, larger New Caledonian *Rhacodactylus* exhibit much lower tooth locus numbers (see Fig. 4B, C).

In interspecific comparisons tooth size is inversely correlated with tooth number (see Table 1). This is due in part to packing constraints, but also results from the relatively large diastimae that characterise the larger species, and *Rhacodactylus auriculatus* in particular (Fig. 4D).

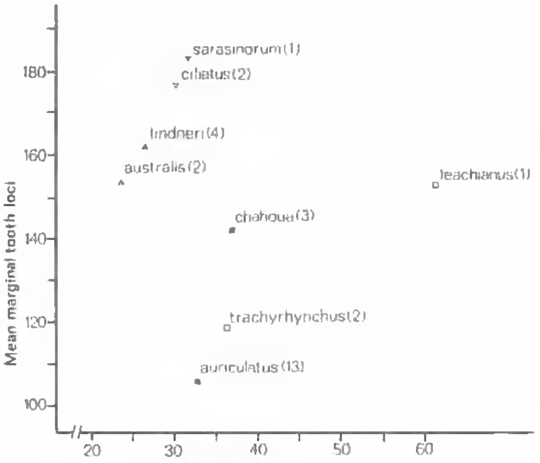


FIG. 3. Graph of mean marginal tooth loci versus mean skull length for eight *Rhacodactylus* species. Number of specimens of each taxon examined is listed parenthetically. Only adult specimens for which accurate tooth locus counts could be made are included (see text for exception of *R. trachyrhynchus*).

In all species, tooth replacement patterns leave at least some loci without functional marginal teeth. In these instances small replacement teeth of the next generation may be seen attached to the alveolar locus. Precise counts of the number of loci undergoing replacement at any time were not possible in the material available, as museum material, especially dry skeletal specimens, may lose teeth through the skeletonization process, storage or shipping. It is noteworthy, however, that premaxillary teeth were rarely absent and that maxillary and dentary tooth rows lacked approximately 20 - 25% of teeth in all taxa except *Rhacodactylus auriculatus*, in which 25 - 30% were lacking.

Within a single species, such as *Rhacodactylus auriculatus*, tooth number increases ontogenetically (Fig. 5) at least until sexual maturity. A more or less steady addition of tooth loci begins during prenatal life and continues until a body size of approximately 95mm SVL (skull length 26mm) is reached. This corresponds roughly to minimal breeding size. Other than absolute size, no differences in juvenile and adult dental morphology were noted in *R. auriculatus*. No sexually related differences in either tooth size or number were noted in this, or any other *Rhacodactylus* species.

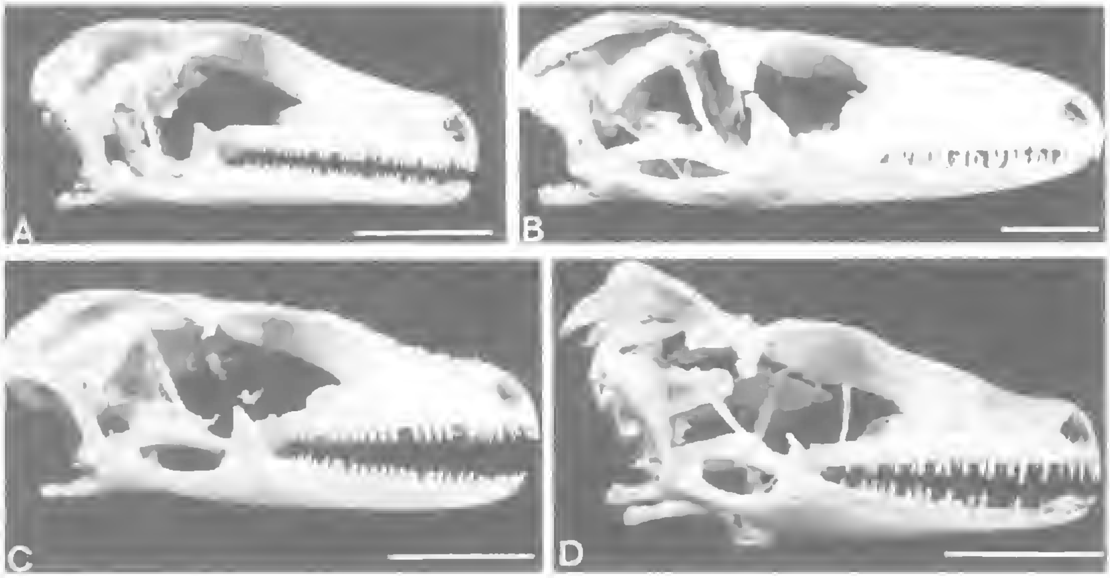


FIG. 4. Right lateral views of the skulls of *Rhacodactylus* spp. illustrating variation in tooth size, number and shape. A. *R. ciliatus* (BM(NH) 86.3.11.4), B. *R. leachianus* (CAS 165890). C. *R. trachyrhynchus* (BM(NH) 85.11.16.7), D. *R. auriculatus* (CAS 165891). In D. the posterior end of the skull is somewhat distorted by the separation of the quadrate, squamosal and parietal bones. Scale bars for all figures = 10mm.

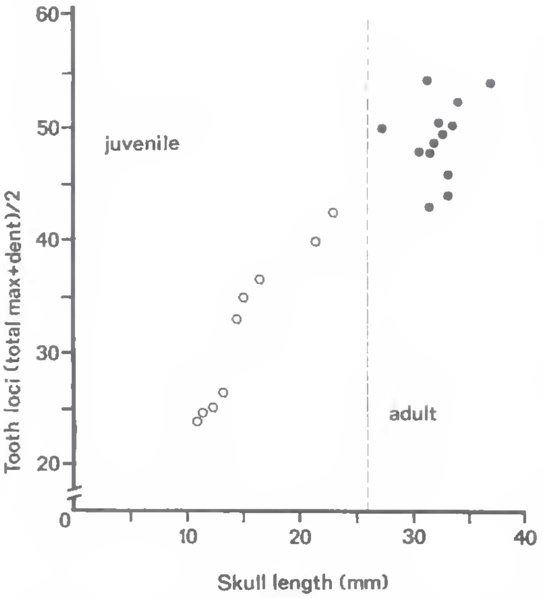


FIG. 5. Graph of mean unilateral tooth loci (maxillary and dentary) versus skull length (measured from tip of snout to occipital condyle) for specimens of *Rhacodactylus auriculatus*. Premaxillary teeth were excluded because of the relative constancy of their number after hatching and subsequent loss of the egg teeth. Dashed line separates juveniles (including pre-hatchlings) (open circles) from adults (closed circles).

EGG TEETH

In all *Rhacodactylus* the number of premaxillary teeth is small and relatively stable. In the largest species and those species with high total tooth counts there are generally nine to eleven premaxillary loci while in *R. auriculatus* seven is the modal number. As in all oviparous geckos, embryos and hatchling *Rhacodactylus* possess only deciduous egg teeth in the premaxillae. These are shed within a few days of eclosion and replaced shortly thereafter by premaxillary teeth essentially identical to those of the adult. Egg teeth were examined in *R. auriculatus* and *R. chahoua*. These structures are about twice the size of the dentary or maxillary teeth. The egg teeth are broad and flattened and project anteriorly (Fig. 6). The presence of egg teeth in the viviparous species *Rhacodactylus trachyrhynchus* has not been confirmed.

TOOTH VASCULARIZATION

A gross examination of vascularization of the mouth cavity of *Rhacodactylus auriculatus* revealed that the entire oral mucosa is supplied by a dense network of blood vessels (Fig. 7). Individual tooth roots are invested with capillary cores which take their origin from the dental branches of the maxillary and mandibular arteries (vessel terminology follows O'Donoghue, 1921, and Oelrich, 1956). These arteries in turn arise from the stapedial artery which ultimately takes its origin from the internal carotid.

DISCUSSION

PHYLOGENETIC IMPLICATIONS

Gecko tooth form (Bauer, 1986) and cuspation (Grismer, 1986, 1987; Sumida and Murphy, 1987) have been employed to a limited extent in phylogenetic analysis. Unfortunately, many of the details of dental structure are difficult to examine without removing teeth for electron microscopy, and as a result only very few taxa have been adequately investigated. Relationships within *Rhacodactylus* proposed by Bauer (1986), largely on the basis of non-dental characters, are not strongly reflected in the evidence from tooth morphology. The sister group status of the *Pseudothecadactylus* species may be confirmed by the similarity of their tooth morphology, but in the absence of comparable data from other carphodactyline geckos their shared features cannot be assumed to be apomorphic. The

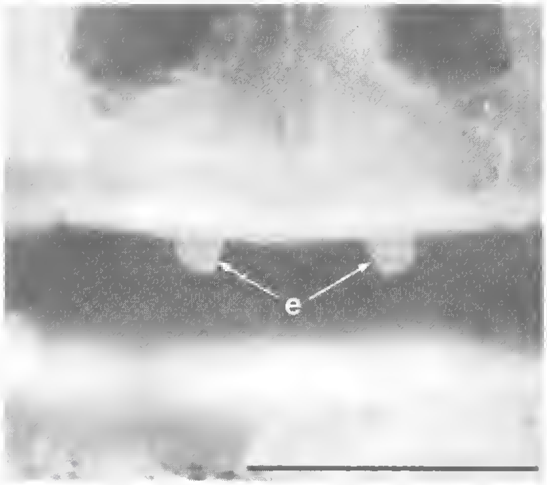


FIG. 6. Egg teeth of a cleared-and-stained pre-hatchling of *Rhacodactylus auriculatus* (AMB, personal collection). Note the orientation and large size of the egg teeth (e) relative to the maxillary and dentary dentition. Scale bar = 1mm.

FIG. 7. Palatal view of a cleared-and-stained Microfil^{TM}-injected *Rhacodactylus auriculatus* (CAS 165897) showing the dense vascularization of the oral mucosa. Tooth roots are served by dental branches of the maxillary and mandibular arteries. Scale bar = 5mm.

autapomorphic elongate caniniform teeth of *Rhacodactylus auriculatus* would appear to be unique among the Diplodactylinae, but provide no clues to affinity. *Rhacodactylus leachianus* and *R. trachyrhynchus* share some features, such as moderately great crown height and recurved crown tips, but differences in cuspation and a lack of corroboration from other characters renders these features of little systematic value. Indeed, the diversity of tooth form among the eight taxa examined is unexpected and, if the monophyly of the *Rhacodactylus/Pseudothecadactylus* lineage is accepted, then function rather than phylogeny may be supposed to play the greatest role in the determination of tooth form.

FUNCTION

Dietary correlates of dental morphology have long been presented as evidence of a tightly coupled form-function complex. Mammals, including bats (Freeman, 1979, 1981, 1988) and sabre-toothed cats (Akersten, 1985), among many others, have been the subject of intensive analysis. Lizards, largely because of the mistaken belief that their dentitions are simple, homodont and isodont have received less attention (Edmund, 1969; Vorobyeva and Chugunova, 1986). None the less, iguanids (Hot-

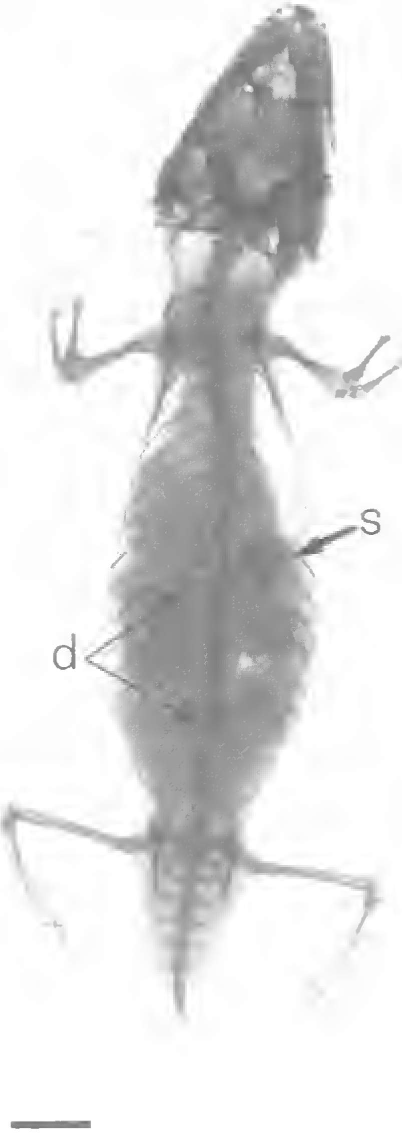


FIG. 8. Radiograph of an adult female *Rhacodactylus auriculatus* (AMS R 78121) illustrating the presence of a whole snail shell (s) as well as chitinous arthropod debris (d) in the digestive tract. Scale bar = 10mm.

ton, 1955; Montanucci, 1968) macroteids (Presch, 1974; Dalrymple, 1979; Dessem, 1985), agamids (Cooper et al., 1970; Chugunova et al., 1987) and varanids (Lönnberg, 1903; Cowles, 1930) have received some attention in this regard. Among gekkotans functional dental morphology has only recently begun to be explored (Sumida and Murphy, 1987; Patchell and Shine 1986a,b - pygopodids).

The diversity of dental form found within *Rhacodactylus* provides the opportunity to make predictions about dietary preferences on the basis of data from other lizard groups. The elongate caniniform teeth of *R. auriculatus* are typical of tetrapods that feed primarily on soft-bodied prey items. Such pointed, elongate 'fangs' have been reported elsewhere in the teiid *Callopistes flavipunctatus* (Presch, 1974) and the iguanid *Gambelia wislizenii* (Hotton, 1955), both of which feed on vertebrate prey. Among other geckos Sumida and Murphy (1987) reported that *Gekko* and *Chondrodactylus*, again vertebrate predators, possessed upright, partly developed cusps implying that penetration rather than crushing or restraining functions are paramount in these forms. A similar morphology is seen in moth-feeding molossid bats (Freeman, 1979). The constricted 'neck' of *Rhacodactylus auriculatus* teeth (Fig. 2) may represent a preformed zone of weakness at which breakage may occur during excessive prey movement. Gecko teeth in general have been characterised as brittle (Vorobyeva and Chugunova, 1986) and high replacement rates (Edmund, 1969) have been interpreted as a compensation for this. In *R. auriculatus* facilitated crown loss may insure that the dental lamina itself is not damaged by trauma resulting from rapid root movement. Such breakage phenomena may be akin to the dietary-related ones evident in predatory mammals (Van Valkenburgh, 1988), where dental fracture is associated with occasional, unpredictable high stresses.

Available information on diet confirms that *Rhacodactylus auriculatus* feeds, at least in part, on soft-bodied prey. Bauer and DeVaney (1987) recorded the remains of the small carphodactyline *Bavayia sauvagii* from the stomach of this species. The species is also known to eat insects (Bauer and DeVaney, 1987) and snails (Fig. 8) as well as flowers (Bavay, 1869) but there are no obvious dental correlates of these foods, suggesting that vertebrate prey (and perhaps large, soft-bodied insects) comprise the bulk of the diet. This prediction may be evaluated by analysing the gut contents of the many specimens available in museum collections. Alternatively, however, a preformed zone of weakness may be associated with rare (Gretener 1984) but significant events and may represent an example of what may initially appear to be an 'excessive construction' (Gans, 1979).

The recurved teeth of *Rhacodactylus trachyrhynchus* and especially *R. leachianus* are rare among geckos. Sumida and Murphy (1987) did not acknowledge their existence, while Grismer (1986) reported them only in *Hemidactylus flaviviridis*, *Hemitheconyx* spp. *Phelsuma sundbergi* and *Tarentola americana*. Normally, recurved teeth are associated with grasping or holding prey during the ingestion cycle (see Wake and Wurst, 1977). However, such teeth are also believed to concentrate bite force at the recurved point (Gans 1974) and in non-geckos are frequently associated with multiple cuspation (see Sumida and Murphy, 1987). In *Rhacodactylus leachianus* there is but a single cusp (Fig. 1C) and this is parallel to the tooth row. In this species the teeth appear best suited to piercing and shearing motions, again probably associated with soft-bodied prey. The large size of this gecko and its ability to overpower prey may obviate the need for the more piercing/holding dentition of *R. auriculatus*, or alternatively it may permit finer intraoral processing of very large prey items. Little is known of the diet of this species in the wild, although small birds are known to be taken (Roux, 1913). In captivity mice (Bauer and DeVaney, 1987) and fruit (Mertens, 1964) are accepted. Small vertebrates, insects and fruit (Bauer, 1986) have been proposed as the food of *Rhacodactylus trachyrhynchus* but the native diet remains unconfirmed. Tooth morphology and the apparent ecological position of this, and other large *Rhacodactylus* species as dominant predators in New Caledonia, however, strongly suggest that this species could exploit saurian or avian prey.

The teeth of the remaining species of *Rhacodactylus*, although varying in cuspation, are very small and tightly packed (Fig. 4A). Bicuspid teeth in particular, such as those of *R. ciliatus*, have been associated with a crushing function useful for hard bodied insects. Small blunt teeth, as in *Pseudothecadactylus* spp. have also been associated with insectivory, especially in regard to smaller, softer taxa (Hotton, 1955). A somewhat similar morphology characterises *Coleonyx* spp. (Kluge, 1962) which are known insectivores. Comparable analogues also occur

TABLE 1. Tooth number and size in adult *Rhacodactylus*.

Taxon (n)	Total tooth Loci ($\bar{x}$)	Maximum Crown height (mm)	Maximum Crown width (mm)
NEW CALEDONIAN			
R. auriculatus (13)	105.5	1.55	0.71
R. chahoua (3)	142	0.75	0.45
R. ciliatus (2)	177	0.50	0.40
R. leachianus (1)	153	1.60	0.70
R. sarasinorum (1)[1]	183	0.45	0.40
R. trachyrhynchus (2)[2]	119.5	1.00	0.43
AUSTRALIAN			
R. (*Pseudothecadactylus*) *australis* (2)[1]	153.5	0.40	0.37
R. (*P.*) *lindneri* (4)[1]	162	0.45	0.40

[1] Tooth dimensions estimated from radiographs. [2] Data come from sub-adult specimens.

in mammalian insectivores (see Freeman, 1979, 1988).

Little is known of the diet of the smaller species of *Rhacodactylus* (including *Pseudothecadactylus*), but it is likely that all consume insects. In captivity *Rhacodactylus chahoua* accepts both fruit and insects (Bauer, 1985). *Rhacodactylus* (*Pseudothecadactylus*) *lindneri* includes at least some vertebrates in its diet and has been observed to feed on *Gehyra* species in Kakadu National Park (Bauer, 1986).

Although well-defined characteristic dentitions appear to typify durophagous (Lönnberg, 1903; Dalrymple, 1979; Vorobyeva and Chugunova, 1986) and herbivorous (Hotton, 1955; Montanucci, 1968; Cooper et al., 1970; DeQueiroz, 1987) lizards, mechanical constraints on the processing of other food types, including insects and vertebrates seem to be less restrictive. Thus dietary preference may be reflected in dentition, but, depending on size and phylogenetic limitations, several tooth morphologies may be equally efficacious in processing the same prey type (Chugunova et al., 1987). Much of the difficulty in understanding the correlation of diet and dentition stems from the fact that little is really known of the properties of different food types (Freeman, 1988) or of the dietary scope of most lizards. Indeed, most geckos, and certainly all *Rhacodactylus*, take a variety of prey types. Dentitions must not, therefore, be expected to be optimally constructed to deal with single prey types. Rather they may be predicted to present a compromise solution to the problem of a varied diet, with an emphasis on those features most suited to the processing of food items that comprise the greatest bulk of the consumed prey, or those imposing the greatest mechanical stress (Gans, 1979; Van Valkenburgh and Ruff, 1987). Future additions to our knowledge of the diet of *Rhacodactylus* spp. may confirm or clarify the predictions stemming from the details of morphology discussed here.

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